Influence of Odonate Intermediate Host Ecology on the Infection Dynamics of *Halipegus* spp., *Haematoloechus longiplexus,* and *Haematoloechus complexus* (Trematoda: Digenea)

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ABSTRACT: The prevalences and relative densities of *Halipegus* spp., *Haematoloechus longiplexus,* and *Haematoloechus complexus* metacercarial infections in anisopteran (dragonfly) and zygopteran (damselfly) odonate intermediate hosts were examined. These measures of infection were compared in relation to the ecological habits of the host species. Also, the extent of second intermediate host specificity was compared between the 2 species of *Haematoloechus.* Eighteen species ($N = 934$) of odonates were dissected and examined for metacercariae. *Halipegus* spp. generally had the highest prevalences and relative densities of infection when compared with *Haematoloechus* spp. in this system. Except for 1 host species, no significant differences in levels of infection were found between the 2 species of *Haematoloechus* in anisopterans. *Haematoloechus longiplexus* was a second intermediate host specialist, being found in anisopteran odonates only. In contrast, *Haematoloechus complexus* was a generalist and was found in both anisopteran and zygopteran hosts. Differences in infections among host species suggest that variations in odonate ecology are sufficient to influence the suitability of larval odonates to serve as intermediate hosts for these frog trematodes.

KEY WORDS: *Halipegus* spp., *Haematoloechus longiplexus, Haematoloechus complexus,* odonate, host specificity.

Bush et al. (1993) argued for the increased consideration of invertebrate intermediate hosts when investigating parasitic helminth community dynamics. Traditionally, vertebrate definitive hosts have received most of the attention in these analyses (Esch et al., 1990), although community studies of intramolluscan trematodes have received considerable attention recently (Kuris, 1990; Sousa, 1990, 1993; Fernandez and Esch, 1991a; Williams and Esch, 1991; Snyder and Esch, 1993; Esch and Fernandez, 1994; Lafferty et al., 1994). Few studies have concentrated on parasites in invertebrate second or third intermediate hosts, i.e., those that have a closer ecological association with the definitive host, because the parasites rely on predator–prey pathways for transmission.

Halipegus occidualis Stafford, 1905, is a hemiurid trematode that uses odonate (Insecta: Odonata; i.e., dragonfly and damselfly) naiads as third intermediate hosts. Naiads infected with metacercariae are ingested by the green frog, *Rana clamitans,* in which the parasites mature in the buccal cavity under the tongue (Goater et al., 1990). *Halipegus eccentricus* Thomas, 1939, is similar to *H. occidualis,* except that adults mature in the eustachian tubes of the ranid definitive host. The life cycle of *H. eccentricus* has traditionally been thought to include only 3 hosts, with tadpoles ingesting infected microcrusta-

ceans (the second intermediate host) (Thomas, 1939). Thomas concluded that metacercariae would then reside in the host's stomach until the tadpole metamorphosed into an adult frog, at which time the worm would migrate up the esophagus to the eustachian tubes, where it would mature and live as an adult (Thomas, 1939). However, unpublished field data from our laboratory on the recruitment of this parasite into its definitive host (*R. clamitans*) suggest that *H. eccentricus* metacercariae also can be found in odonates, which presumably act as third intermediate hosts. This would make the life cycle of *H. eccentricus* similar to that of its congener, *H. occidualis.* Thus, in habitats such as Charlie's Pond, where both congeners could be present within larval odonates, and because they are morphologically indistinguishable, they are referred to as *Halipegus* spp. for the purposes of this study.

Haematoloechus complexus Seely, 1906, and *H. longiplexus* Stafford, 1902, are frog lung flukes that use odonate naiads as second intermediate hosts. A number of previous studies have examined odonates for infections with *Halipegus* (Willey, 1930; Krull, 1935; Rankin, 1944; Macy et al., 1960; Kechemir, 1978; Goater, 1989; Fernandez, 1991) and *Haematoloechus* (Krull, 1930, 1931, 1932, 1933, 1934; Ingles, 1933; Grabda, 1960; Dronen, 1975, 1978; Bourgat and Kulo,

1979). However, these efforts predominantly have been surveys of odonate naiads as intermediate hosts in life history studies. Recently, Snyder and Janovy (1994) examined the second intermediate host specificity for 2 species of *Haematoloechus* and provided experimental evidence of important differences in host specificity between the species. However, field evidence for specificity of *Haematoloechus* spp. in odonates is lacking.

In this paper, we examine the prevalences and relative densities (as defined in Margolis et al., 1982) of *Halipegus* spp., *H. complexus,* and *H. longiplexus* metacercarial infections in several species of anisopteran (dragonflies) and zygopteran (damselflies) odonates in relation to the different ecological habits of these hosts. We also compare the prevalences and relative densities of 2 species of *Haematoloechus* to investigate whether strong second intermediate host specificity can be observed in samples of field-collected hosts.

Materials and Methods

Odonate naiads were sampled from several sites within Charlie's Pond, a 2-hectare pond in the Piedmont area of North Carolina, U.S.A., from June 1992 to June 1993. Because this study was associated with a more extensive investigation of trematode population dynamics in the definitive host, *Rana clamitans,* naiads were not sampled in the winter months (November–March) when frogs were inactive and not recruiting parasites. Odonates were collected using an aquatic sampling net and a 2-mm² mesh screen, placed in jars of pond water, and returned to the laboratory. Individuals were isolated at room temperature in 65-ml plastic jars filled with pond water. Naiads were examined under a dissecting microscope within 2 days of capture and identified to species according to Huggins and Brigham (1982). All parts of the odonate body were examined for metacercariae. *Halipegus* spp. were always found in the midgut of the naiads. *Haematoloechus complexus* was found in all parts of the body, occurring in a thin, hyaline cyst in the abdominal cavity, legs, and head. *Haematoloechus longiplexus* was unencysted and was always found associated with the branchial basket/respiratory structures of anisopteran odonates. Specimens of parasites are deposited in the U.S. National Parasite Collection, Beltsville, Maryland 20705, as follows: *Halipegus* spp. (USNPC 85276), *Haematoloechus longiplexus* (USNPC 85277), and *Haematoloechus complexus* (USNPC 85278).

Data used to calculate prevalences were analyzed using chi-square (Zar, 1984). Relative density data were analyzed with an analysis of variance (ANOVA) using Systat (Wilkinson, 1989). Differences between groups were determined using Tukey's honestly significant difference (HSD) test. Probability values less than 5% ($P < 0.05$) were considered statistically significant. In a few instances, relative density data were distributed nonnormally and were analyzed with a Kruskal-Wallis nonparametric ANOVA. Due to the robustness of ANOVA, results from the nonparametric and parametric tests were consistent; thus, results are reported only from the parametric ANOVA for consistency.

Results

Eighteen species of odonates, representing 5 families, were examined ($N = 934$). Those species with sample sizes adequate for statistical analysis are shown in Table 1. Other anisopterans that were examined, but not included in Table 1, were *Boyeria vinosa* ($N = 6$; 4 infected with *Halipegus* spp., 1 infected with *H. complexus*) (Aeschnidae), *Neurocordulia alabamensis* ($N = 1$) (Corduliidae), *Cerithemis monomelaena* ($N = 1$), *Libellula deplanata* ($N = 2$), and *Perithemis seminole* ($N = 2$) (Libellulidae). Additional zygopterans included *Enallagma exsulans* ($N = 15$; 4 infected with *Halipegus* spp., 2 infected with *H. complexus*), *En. signatum* ($N = 1$), and *Ischnura verticalis* ($N = 1$; 1 infected with *Halipegus* sp.) (Coenagrionidae).

Halipegus spp. generally were the most prevalent of the 3 trematode species (Table 1). Prevalences ranged from 55% in *Epitheca cynosura* to 3% in *Gomphus exilis,* which was significantly lower than in all other hosts ($\chi^2 = 47.9$, df = 1, $P < 0.001$). There was no significant difference in *Halipegus* spp. infection among *Ep. cynosura, L. luctuosa, En. traviatum, En. basidens,* or *Erythemis simplicicollis* ($\chi^2 = 2.28$, df = 4, $P > 0.05$); infection with *Halipegus* spp. in this group was significantly higher than in other hosts. Within individual host species, the prevalence of *Halipegus* spp. was significantly higher than the 2 species of *Haematoloechus* ($P < 0.05$) except in *G. exilis* ($\chi^2 = 1.24$, df = 2, $P > 0.05$) and *I. posita* ($\chi^2 = 0.27$, df = 2, $P > 0.05$), for which there were no differences in prevalence of all 3 trematodes. Likewise, for *L. luctuosa* there was no difference between the prevalences of *Halipegus* spp. (54%) and *H. longiplexus* (41%) ($\chi^2 = 1.43$, df = 2, $P > 0.05$).

The relative density of *Halipegus* spp. in *Er. simplicicollis* was significantly higher than in all other hosts except *En. traviatum* and *Ep. cynosura* (Table 1; Tukey HSD, $P < 0.05$). *Halipegus* spp. generally had the highest relative densities of the 3 trematodes within individual host species as well. There were no significant differences among relative densities of any parasite for *A. fumipennis, G. exilis,* and *I. posita.* Only in *L. luctuosa* was the relative density of *Halipegus* spp. significantly lower than *H. longiplexus* ($t = $

Table 1. Total prevalence, relative density, and range of infection of odonate naiads infected with metacercariae.

Odonate (habit*)	N	*Halipegus* spp.		*Haematoloechus longiplexus*		*Haematoloechus complexus*	
		No. infected (%)	Relative density ± SE (range)	No. infected (%)	Relative density ± SE (range)	No. infected (%)	Relative density ± SE (range)
Suborder Anisoptera							
Gomphidae							
Gomphus exilis (B)	301	8 (3)	0.03 ± 0.01 (0–2)	13 (4)	0.05 ± 0.02 (0–2)	11 (4)	0.04 ± 0.01 (0–2)
Corduliidae							
Epicordulia princeps (C, S)	68	21 (31)	0.9 ± 0.2 (0–9)	9 (13)	0.2 ± 0.08 (0–4)	5 (7)	0.7 ± 0.3 (0–1)
Epitheca cynosura (C, S)	31	17 (55)	1.5 ± 0.4 (0–9)	5 (16)	0.4 ± 0.2 (0–5)	5 (16)	0.3 ± 0.1 (0–4)
Libellulidae							
Erythemis simplicicollis (S)	90	38 (42)	2.7 ± 0.6 (0–40)	3 (3)	0.08 ± 0.05 (0–3)	9 (10)	0.3 ± 0.6 (0–7)
Libellula cyanea (S)	200	76 (38)	0.6 ± 0.06 (0–4)	36 (18)	0.6 ± 0.2 (0–19)	32 (16)	0.3 ± 0.06 (0–7)
Libellula luctuosa (S)	37	20 (54)	0.9 ± 0.2 (0–5)	15 (41)	1.0 ± 0.3 (0–9)	8 (22)	0.6 ± 0.3 (0–9)
Suborder Zygoptera							
Coenagrionidae							
Argia fumipennis (C, S)	54	19 (35)	0.7 ± 0.2 (0–9)	0	0	7 (13)	0.5 ± 0.2 (0–7)
Enallagma basidens (C)	33	15 (46)	1.0 ± 0.3 (0–5)	0	0	5 (15)	0.3 ± 0.1 (0–3)
Enallagma traviatum (C)	41	20 (49)	1.7 ± 0.4 (0–10)	0	0	4 (10)	0.3 ± 0.2 (0–7)
Ischnura posita (C)	50	10 (20)	0.3 ± 0.08 (0–3)	0	0	8 (16)	0.3 ± 0.1 (0–4)

* Ecological habits of odonates: B = burrower; C = climber; S = sprawler.

Table 2.   Prevalence and relative density of infection of odonate naiads grouped by the ecological habit of the host. Only those species having a singular ecological habit designation are included.

Ecological habit	N	Halipegus spp.		Haematoloechus longiplexus		Haematoloechus complexus	
		Prevalence (%)	Relative density ± SE	Prevalence (%)	Relative density ± SE	Prevalence (%)	Relative density ± SE
Burrower*	301	2.7	0.03 ± 0.01	4.3	0.05 ± 0.02	3.7	0.04 ± 0.01
Climber†	124	36.3	1.0 ± 0.2	0	0	13.7	0.3 ± 0.9
Sprawler‡	327	41.0	1.2 ± 0.2	16.5	0.5 ± 0.1	15.0	0.3 ± 0.06

* Burrower = *Gomphus exilis.*

† Climbers = *Enallagma basidens, Enallagma traviatum, Ischnura posita.*

‡ Sprawlers = *Erythemis simplicicollis, Libellula cyanea, Libellula luctuosa.*

2.25, df = 72, $P < 0.025$). There was no significant difference in densities of *Halipegus* spp. and *H. longiplexus* within *L. cyanea* ($t = 0.1$, df = 398, $P > 0.05$).

Haematoloechus longiplexus infected anisopteran odonates only (Table 1). For anisopteran hosts, there were no significant differences in either the prevalence or the relative density of infection with *H. longiplexus* and *H. complexus* except in *L. luctuosa.* In the latter host species, the prevalence of *H. longiplexus* (41%) was significantly higher than that of *H. complexus* (22%; $\chi^2 = 3.1$, df = 1, $P < 0.05$). Similarly, the relative density of *H. longiplexus* was significantly higher than for *H. complexus* ($t = 6.11$, df = 72, $P < 0.001$).

In contrast to its congener, *H. complexus* infected both anisopteran and zygopteran odonates (Table 1). The prevalence of *H. complexus* in all species of zygopterans was lower than that of *Halipegus* spp. except in *I. posita* ($\chi^2 = 0.27$, df = 1, $P > 0.05$). There were no significant differences in relative densities of infection with *H. complexus* and *Halipegus* spp. for *I. posita* ($t = 0.51$, df = 98, $P > 0.05$) and *A. fumipennis* ($t = 0.88$, df = 106, $P > 0.05$). However, there were significantly lower densities of *H. complexus* than *Halipegus* spp. in *En. basidens* and *En. traviatum* (Table 1; Tukey HSD, $P < 0.05$).

There were no significant differences in the prevalence ($\chi^2 = 0.74$, df = 1, $P > 0.75$) or relative density ($t = 1.48$, df = 448, $P > 0.5$) of infection with *H. occidualis* between sprawling and climbing odonate species (Table 2). Likewise, there were no significant differences in the prevalence ($\chi^2 = 0.09$, df = 1, $P > 0.9$) or relative density ($t = 0.22$, df = 449, $P > 0.5$) of infection with *H. complexus* between these groups. When the sprawling and climbing habits were pooled and collectively compared with levels of infec-

tion of the burrowing habit (i.e., *G. exilis*), there were highly significant differences in both the prevalence and relative density (respectively) of infection for *H. occidualis* ($\chi^2 = 133.0$, df = 1, $P < 0.001$; $t = 8.4$, df = 750, $P < 0.001$), *H. longiplexus* ($\chi^2 = 32.1$, df = 1, $P < 0.001$; $t = 5.3$, df = 626, $P < 0.001$), and *H. complexus* ($\chi^2 = 24.1$, df = 1, $P < 0.001$; $t = 3.3$, df = 750, $P < 0.001$).

Discussion

Halipegus spp. generally had the highest prevalences and relative densities of infection when compared with *Haematoloechus* spp. in this system. The prevalence of *Halipegus* spp. ranged from a high of 55% in *Ep. cynosura* to a low of 3% in *G. exilis,* a species that consistently had low prevalences and relative densities of all 3 parasites. Of all the species that were sampled, *Gomphus exilis* is the only burrower; i.e., the naiads burrow beneath the surface of the pond bottom mud, sand, or sediment (Huggins and Brigham, 1982). This life style or ecological "habit" would seem to restrict predation by this species on large numbers of infected ostracods (in the case of *Halipegus* spp.) or to reduce exposure of the host to the motile cercariae of *Haematolochus* spp., relative to the other species of odonates. In contrast, all other odonate species had prevalences of *Halipegus* spp. that were at least 20%. These species represent 2 other ecological habits: climbers (*A. fumipennis, Enallagma* spp., *I. posita, Ep. cynosura*) and sprawlers (*Epi. princeps, Er. simplicicollis, Libellula* spp.) (Huggins and Brigham, 1982). Climbers are active predators that stalk their prey when foraging. Sprawlers are ambush predators, sitting and waiting for prey to move close to them (Huggins and Brigham, 1982). Species representing these latter 2 habits have relatively greater exposure

to the water column, including infected ostracods and motile cercariae.

There were no significant differences in patterns of infection between climbers and sprawlers. However, when collectively compared with the burrowing habit, the climber and sprawler habits had significantly greater prevalences and relative densities of infection of all 3 species of trematode. In light of this, we suggest that the ecological habit of the intermediate host may reflect real biological limits with respect to which species may play an important role in the dynamics of the parasite's life cycle. Given that all of these species were clearly susceptible to infection (notwithstanding the absence of *H. longiplexus* from zygopteran hosts), we feel that the differences in levels of infection among host species were primarily due to ecological/habitat determinants rather than patterns of host phylogenies (Bush et al., 1990). Thus, because of the sometimes large differences in levels of infection between hosts representing different ecological habits, care must be taken when generalizations are made with respect to a particular host "group." For example, Dronen (1978) examined several anisopteran and zygopteran odonate species, treating them as a single group because they reportedly served equally well as second intermediate hosts for *H. coloradensis* (=*H. complexus*; Kennedy, 1981). However, inspection of the present data suggests there is substantial variability in the suitability of a particular species as a host. Furthermore, much of this variability can be attributed to simple differences in the ecological habits of the hosts. When considering *H. longiplexus,* for example, treating both anisopteran and zygopteran odonates as a single group would have a serious impact on the assessment of prevalence and relative density of infection, given the strong specificity of this parasite for anisopteran naiads. Clearly, ecological habits of intermediate hosts must be considered when examining patterns of infection at the level of the component community.

Differences in host specificity were observed between *H. longiplexus* and *H. complexus*. *Haematoloechus longiplexus* infected only anisopteran odonates, whereas *H. complexus* infected both anisopterans and zygopterans. The apparent restriction of *H. longiplexus* to anisopterans in this system is in contrast to the work of Krull (1932), in which he described this species as occurring in the zygopteran *Lestes vigilax*. As we have no reason to doubt the experimental infec-

tions of Krull (1932), this discrepancy suggests that levels of host specificity may be more fine tuned than at the level of taxonomic suborders (i.e., anisopteran vs. zygopteran hosts). Because *Lestes* sp. does not occur in Charlie's Pond, potentially susceptible zygopteran hosts may not be present in this system. These differences also imply that regional differences in invertebrate intermediate host use may exist.

Except for 1 host species (*L. luctuosa*), there were no differences in either the prevalence or relative density of infection with *H. longiplexus* and *H. complexus* in anisopteran hosts. The similarities between the 2 congeners are interesting because the patterns do not reflect those seen at the level of the first intermediate hosts. In Charlie's Pond, *H. complexus* occurred in over 15% of *Physa gyrina,* its first intermediate host (Snyder and Esch, 1993). In contrast, *H. longiplexus* infected less than 1.5% of the snail *Helisoma anceps* for any given month (Fernandez and Esch, 1991b). We recognize that differences of this sort could be a result of different population sizes of the first intermediate hosts, but as population densities of the snail species have not been estimated, no conclusive comparisons are possible at this time. Instead, we suggest that despite the greater prevalence of *H. complexus* in its first intermediate host (*P. gyrina*), the similarity in the levels of infection with *H. longiplexus* and *H. complexus* in their second intermediate hosts (odonates) is a function of differing host specificities of these parasites.

Recently, Snyder and Janovy (1994) demonstrated that *H. complexus* is a second intermediate host generalist; this trematode was able to infect 9 arthropod species (representing 2 subphyla and 3 insect orders) exposed to cercariae. Whereas they did not test *H. longiplexus* in their study, a pattern similar to *H. longiplexus* was seen with *H. medioplexus*: it too infected only anisopteran naiads (Snyder and Janovy, 1994). They suggested that anuran definitive hosts might have a better chance of ingesting a food item infected by the generalist (*H. complexus*) because this parasite can infect a wider range of prey items. Using this logic, we suggest that, given a finite number of cercariae shed by an infected snail, a generalist parasite species would be expected to have a lower prevalence of infection in any particular second intermediate host species when compared with a parasite that was a specialist on that second intermediate host species. Assuming that *H. complexus* uses several other

aquatic arthropods in Charlie's Pond, we pro-
pose that the similarities in infection of anisop-
teran odonates with *H. longiplexus* and *H. com-
plexus* in this system are created by the "dilu-
tion" of cercariae of *H. complexus* into other
types of hosts (e.g., zygopterans). This would ef-
fectively counterbalance the initially large dif-
ference in prevalences of these parasites in their
first intermediate hosts. Thus, the anisopteran-
specialist *H. longiplexus* may be as prevalent in
anisopteran hosts as the generalist *H. complexus,*
despite the cercariae being shed from a much
smaller proportion of its respective snail host.

Despite the variable levels of infection among
odonate species, which, in this system, can be
attributed primarily to different ecological hab-
its, it does appear that a wide variety of the odo-
nates could serve as suitable intermediate hosts.
All of the trematodes in the present study are
actively recruited by, and mature in, ranid frogs.
Which odonate species act as the primary inter-
mediate hosts in this system remains unknown.
Presumably, species such as *Er. simplicicollis* and
L. cyanea play an important role in the trans-
mission dynamics of these parasites; they are
abundant in the pond and have relatively high
prevalences and relative densities of infection.
For example, up to 40 metacercariae have been
observed in 1 individual of *Er. simplicicollis,*
which, if ingested by a frog, could represent an
"instant" infrapopulation in the definitive host.
On the other hand, the burrowing *G. exilis,* al-
though abundant in the pond (representing 32%
of individuals sampled), consistently had the
lowest levels of infection of any host sampled
and thus would not be expected to contribute
greatly to the transmission dynamics of these
trematodes. Nevertheless, given the potentially
large number of hosts that could be used, these
parasites may be successfully "hedging their bets"
against barriers to transmission and local ex-
tinction (Bush and Kennedy, 1994).

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